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Analysis of Time-Dependent Integrodifference Population Models

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May, 2013

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Abstract

The population dynamics of species with separate growth and dispersal stages can be described by a discrete-time, continuous-space integrodifference equation relating the population density at one time step to an integral expression involving the density at the previous time step. Prior research on this model has assumed that the equation governing the population dynamics remains fixed over time, however real environments are constantly in flux. We show that for time-varying models, there is a value Λ that can be computed to determine a sufficient condition for population survival. We also develop a framework for analyzing persistence of a population for which growth and dispersal behavior alternate predictably throughout time. Finally, we consider a number of time-varying models that include randomness.

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Chapter 1

Introduction

1.1 Motivation

Humans depend on biodiversity for trade, sustenance, pharmaceuticals, and entertainment, not to mention the ethical imperative of wildlife protection (Pearce, 1991). However, Earth's biodiversity is under serious threat. The International Union for Conservation of Nature lists 11,167 species as threatened, which is likely an underestimate due to insufficient information (Dirzo and Raven, 2003). The current rate of extinction is estimated to be several hundred times the background rate, making this era comparable to many of the historical mass extinction events if current rates continue (Dirzo and Raven, 2003). In fact, extinction rates are projected to increase as the human population continues to grow and put increased demand on Earth's resources (Dirzo and Raven, 2003). Many sources agree that the primary cause of threat is habitat loss and degradation, followed by direct exploitation and competition with invasive non-native species (Dirzo and Raven, 2003; Tudge, 1992). How can we ensure that threatened populations are able to survive in a limited habitat, or that non-native species will not overwhelm native populations?

Population models are invaluable to conservation ecology because they help us predict the likely impact of environmental change on a given population. In this paper, we consider a population model for species that have separate growth and dispersal stages. This means that the population goes through periods of time when individuals disperse and settle in new locations and periods when the population grows (according to some function of its current density) but does not disperse. Many plants demonstrate this pattern of growth and dispersal, as well as a variety of arthro-

pods (insects, arachnids, and crustaceans) (Howe and Smallwood, 1982; Hassel, 1978). Furthermore, this paper examines populations living in a bounded habitat—a region with suitable living conditions surrounded by regions that are uninhabitable (for example, due to habitat loss). In such an environment, individuals may disperse out of the habitable region and are then considered lost to the population, but no individuals can enter the population from outside.

One interesting kind of population that we will consider is one subjected to a unidirectional flow, such as species like the southern bull-kelp in New Zealand that live in a current or river environment (Collins et al., 2010). This unidirectional flow will tend to bias the dispersal of the population in one direction, which, along with the bounded domain, gives rise to the *drift paradox*—the phenomenon of populations surviving in a limited habitat when they are being continually washed out of it (Lutscher et al., 2005).

Mathematical models help us study the drift paradox, as well as a number of other important ecological questions. We may wish to know whether a population with known (experimentally determined) growth and dispersal behavior will survive or go extinct if introduced to a certain habitat. Related to this are the *critical domain size*, the minimum size that a habitable domain must be for a population to survive, and the *spreading speed*, the rate at which the population moves into a previously uninhabited region (Lutscher et al., 2005; Jacobsen et al., 2013). This research provides a mathematical framework to study how limiting a species' habitat may affect the species' survival or whether a nonnative species will thrive or go extinct in a particular environment.

Previous research in this area has focused on time-independent population models, which assume that a population's growth and dispersal behavior remain constant over time (Kot and Schaffer, 1986; Van Kirk and Lewis, 1997; Lutscher et al., 2005). However, in reality such features are unlikely to be constant, but may have seasonal change, random variation, or other time-dependence. This research examines a variety of models for population growth incorporating factors that change over time. The aim of this research is to make population models more realistic and therefore more useful for answering important ecological questions.

1.2 Mathematical Model

Population growth is frequently modeled through reaction-diffusion equations, which assume that a population is continually growing and dispersing at the same time. However, since we are interested in studying species with separate growth and dispersal stages, an integrodifference population model is more accurate (Kot and Schaffer, 1986; Van Kirk and Lewis, 1997). The integrodifference equation models the population density at discrete points in time, and the density at each time step depends on the density at the previous time step. If $n_t(x)$ is the population density at position x at the end of the dispersal period in the t^{th} time step, then a general time-independent model for the population growth is

$$n_{t+1}(x) = \int_{\Omega} K(x, y) f(n_t(y)) dy$$

where Ω is the habitable domain, f is the growth function, and $K(x, y)$ is the dispersal kernel, which represents the probability that an individual starting at y will settle at x during the dispersal period. In this model, the growth function f is assumed to be a nonnegative, monotonically increasing function with a fixed point at zero (Jacobsen et al., 2013).

When we consider temporal variation, both the growth function and the dispersal kernel could have time-dependence. The generalized integrodifference model becomes

$$n_{t+1}(x) = \int_{\Omega} K_t(x, y) f_t(n_t(y)) dy$$

where $K_t(x, y)$ is the dispersal kernel and $f_t(x)$ is the growth function at the t^{th} time step. This research focuses on models with predictable time-dependence, such as seasonal variation, as well as models with random variation in parameters associated with growth and dispersal.

Chapter 2

Theoretical Background

2.1 Time-Independent Model

Before developing results for the time-varying integrodifference model, it is necessary to understand the theory behind the time-independent model for the kinds of populations we are studying.

Let $n_t(x)$ be the population density at location x of a species with separate growth and dispersal stages after the t^{th} dispersal period. Let Ω be a bounded region in \mathbb{R}^n representing the habitable domain of this population. During the growth stage, population growth is assumed to depend only on the current local density, so if we say $t + 1/2$ is the time stage immediately following the t^{th} growth period, then

$$n_{t+1/2}(x) = f(n_t(x))$$

where f is nonnegative (because population density cannot be negative), monotonically increasing (because the population is growing), and has a fixed point at zero, since at this point the population cannot grow.

During the dispersal stage, the dispersal kernel, $K(x, y)$, represents the probability density of an individual settling at x from starting position y . Since it is a probability density, K is nonnegative and integrates to one over \mathbb{R}^n , and we furthermore assume that it is continuous. In this model, individuals may freely disperse out of the habitable region, but no individuals enter Ω from outside. Since the dispersal stage follows the growth stage, it will depend upon the population density at time $t + 1/2$. Thus, the population density after the $(t + 1)^{\text{th}}$ dispersal stage is given by

$$n_{t+1}(x) = \int_{\Omega} K(x, y) n_{t+1/2}(y) dy$$

or, equivalently,

$$n_{t+1}(x) = \int_{\Omega} K(x, y) f(n_t(y)) dy \quad (2.1)$$

where Equation 2.1 is the general form of the time-independent integrodifference population growth model. This integrodifference model was first studied in an ecological setting by Kot and Schaffer (1986). However, there have since been many extensions to the research, including applications to predator-prey models by Neubert et al. (1995), fragmented habitats by Van Kirk and Lewis (1997), and stream environments by Lutscher et al. (2005).

To understand more about the dynamics of this model, we can rewrite Equation 2.1 as

$$n_{t+1}(x) = F[n_t](x) \quad (2.2)$$

where $F(n_t)(x)$ is the nonlinear Hammerstein operator

$$F[n](x) = \int_{\Omega} K(x, y) f(n(y)) dy \quad (2.3)$$

defined on $C(\overline{\Omega})$, the Banach space of continuous real-valued functions on Ω under the sup norm, defined by $\|u\|_{\infty} = \sup_{x \in \Omega} |u(x)|$ for all $u \in C(\overline{\Omega})$. From a biological standpoint, it is fair to assume that our population densities will be continuous, so this is a natural function space to choose.

A steady-state solution to Equation 2.2 is one that satisfies

$$n_*(x) = F[n_*](x). \quad (2.4)$$

Since f has a fixed point at zero, we see that the population density function $n_*(x) = 0$ satisfies

$$F[n_*](x) = \int_{\Omega} K(x, y) f(0) dy = \int_{\Omega} 0 dy = 0 = n_*(x)$$

and is therefore a steady-state solution. One way we can investigate whether a population survives or goes extinct is by determining the stability of the zero solution. If the zero equilibrium is unstable, the population will grow and survive, but if it is stable, then any small population will tend to zero and become extinct. To analyze the behavior of the system near the zero solution, we look at its linearization about $n_*(x) = 0$:

$$n_{t+1}(x) = \mathcal{L}n_t(x) = R \int_{\Omega} K(x, y) n_t(y) dy \quad (2.5)$$

where $\mathcal{L} = F'(0)$ is the Fréchet derivative and $R = f'(0)$ (see Appendix A for details). To find the eigenvalues of this linear operator, we look at the eigenvalue equation

$$\lambda\phi(x) = R \int_{\Omega} K(x, y)\phi(y)dy. \quad (2.6)$$

For large enough λ , the operator defined by

$$T[\phi] = \frac{R}{\lambda} \int_{\Omega} K(x, y)\phi(y)dy$$

is a contraction mapping (see Appendix B), which tells us that the fixed point at $\phi(x) = 0$ is unique. Since fixed points of T correspond to solutions to Equation 2.6, this tells us that if there exists an eigenvalue, there must exist a principal (largest magnitude) eigenvalue, since larger eigenvalues will force Equation 2.6 to have no nontrivial solution.

In fact, we can say even more about the principal eigenvalue of Equation 2.6. It can be shown that the operator \mathcal{L} is a positive, bounded, compact operator (Appendix C). If we make the further assumption that \mathcal{L} is *strongly positive* (meaning that for any nonnegative $n \in C(\overline{\Omega})$, there exists a power $t(n)$ such that $\mathcal{L}^{t(n)}n > 0$ on all $\overline{\Omega}$) then the Krein-Rutman theorem tells us that \mathcal{L} has a positive principal eigenvalue $\lambda_1 > 0$ corresponding to a nonnegative eigenfunction (Krasnosel'skii, 1964). This implies that the principal eigenvalue can be expressed as the spectral radius of \mathcal{L} , given by the *Gelfand formula*:

$$\lambda_1 = \lim_{t \rightarrow \infty} \|\mathcal{L}^t\|^{1/t} \quad (2.7)$$

where

$$\|A\| = \sup_{\|\phi\|_{\infty}=1} \|A\phi\|_{\infty}$$

is the operator norm.

The principal eigenvalue λ_1 is significant because it determines the stability of the zero steady-state solution. If $\lambda_1 < 1$, then zero equilibrium is linearly stable and the dominant behavior of F near zero is to shrink the population, causing the population to go extinct. On the other hand, if $\lambda_1 > 1$, then the zero equilibrium is unstable, and the dominant behavior of F will be to move small populations away from zero, causing the population to persist (Hardin et al., 1988).

The Gelfand formula in Equation 2.7 leads to several bounds on λ_1 , such as

$$\lambda_1 \leq R, \quad (2.8)$$

$$\lambda_1 \leq \|\mathcal{L}\|, \quad (2.9)$$

and

$$\lim_{t \rightarrow \infty} \left[\int_{\Omega} n_t(x) dx \right]^{1/t} \leq \lambda_1 \quad (2.10)$$

where here $n_t(x) = \mathcal{L}^t n_0(x)$ (Jacobsen et al., 2013). The last inequality, 2.10, shows that the asymptotic geometric growth of the population is bounded above by λ_1 . The Gelfand formula and resulting bounds on the principal eigenvalue are important results for the time-independent model.

If we assume that the dispersal behavior in a subset of the domain does not change as we enlarge Ω , as is the case with common difference kernels of the form $K(x - y)$, then λ_1 is an increasing function of the size of Ω (Jacobsen et al., 2013). This makes intuitive sense, since for a small domain we expect the population loss due emmigration to outweigh population growth, but in a large domain the proportion of the population that disperses to outside the habitable region is proportionally smaller, so growth can dominate. The domain size $|\Omega|$ at which $\lambda_1 = 1$ is the critical domain size, which tells us the minimum domain size needed to ensure survival of the population.

2.1.1 Example with a Symmetric Laplace Kernel

Consider a population in a one dimensional environment, $\Omega = (0, L)$. If this population moves with Brownian motion during the dispersal stage with diffusion coefficient D and settling rate α , then Neubert et al. (1995) show that the density of individuals, $z(t, x)$, follows the differential equation

$$z_t = Dz_{xx} - \alpha z. \quad (2.11)$$

If we want to know how an individual starting at y will disperse during the dispersal period, we use an initial condition of $z(0, x) = \delta(x - y)$, then integrate αz over all time to get the probability that it will have settled at x by the end of the dispersal period (we assume that the time scale for dispersal is large). In other words, $\int_0^\infty \alpha z(t, x) dt$ is precisely the dispersal kernel,

$K(x, y)$. Assuming that $z \rightarrow 0$ as $t \rightarrow \infty$, we can integrate Equation 2.11 over all time to get

$$\begin{aligned} -\alpha\delta(x-y) &= DK_{xx} - \alpha K \\ K_{xx} &= a^2K - a^2\delta(x-y) \end{aligned} \quad (2.12)$$

where $a = \sqrt{\alpha/D}$. The solution to this differential equations is the symmetric Laplace kernel, given by

$$K(x, y) = \frac{a}{2}e^{-a|x-y|}. \quad (2.13)$$

Now, to determine whether the population will survive or go extinct, we want to find the principal eigenvalue of the linear operator \mathcal{L} defined in Equation 2.5. If we have the eigenvalue equation

$$\lambda\phi(x) = R \int_{\Omega} K(x, y)\phi(y)dy \quad (2.14)$$

then we can take the derivative twice with respect to x to get

$$\begin{aligned} \lambda\phi''(x) &= R \int_{\Omega} K_{xx}(x, y)\phi(y)dy \\ &= R \int_{\Omega} (a^2K(x, y) - a^2\delta(x-y))\phi(y)dy \end{aligned}$$

where we have used Equation 2.12 to substitute for K_{xx} . We can simplify this equation to get a second-order ordinary differential equation in ϕ :

$$\begin{aligned} \lambda\phi''(x) &= R \int_{\Omega} (a^2K(x, y) - a^2\delta(x-y))\phi(y)dy \\ &= Ra^2 \int_{\Omega} K(x, y)\phi(y)dy - Ra^2 \int_{\Omega} \delta(x-y)\phi(y)dy \\ \phi''(x) &= a^2\lambda\phi(x) - Ra^2\phi(x). \end{aligned}$$

Thus,

$$\phi''(x) = a^2 \left(1 - \frac{R}{\lambda}\right) \phi(x). \quad (2.15)$$

By Equation 2.14 and Equation 2.13, we know that

$$\phi(x) = \frac{aR}{2\lambda} \int_0^L e^{-a|x-y|}\phi(y)dy$$

and thus

$$\phi'(x) = \frac{a^2 R}{2\lambda} \int_0^L e^{-a|x-y|} \phi(y) dy.$$

By substitution $x = 0$ and $x = L$ into the equations above, we get boundary conditions $\phi'(0) = a\phi(0)$ and $\phi'(L) = -a\phi(L)$. The result of these conditions and Equation 2.15 is a Sturm-Liouville boundary value problem:

$$\begin{cases} \phi''(x) = -A^2\phi(x) \\ \phi'(0) = a\phi(0) \\ \phi'(L) = -a\phi(L) \end{cases} \quad (2.16)$$

where $A = a\sqrt{R/\lambda - 1}$. By Equation 2.8, we know that $\lambda \leq R$, however $\lambda = R$ fails to yield a nontrivial solution to Equation 2.16, so we know that $\lambda < R$. Thus we have the general solution

$$\phi(x) = c_1 \sin(Ax) + c_2 \cos(Ax). \quad (2.17)$$

Applying the first boundary condition yields $c_2 = c_1 A/a$, and applying the second boundary condition yields

$$\begin{aligned} a[c_1 \sin(AL) + c_2 \cos(AL)] + c_1 A \cos(AL) - c_2 A \sin(AL) &= 0 \\ ac_1 \sin(AL) + c_1 A \cos(AL) + c_1 A \cos(AL) - c_1 A^2/a \sin(AL) &= 0 \end{aligned}$$

where we have made the substitution $c_2 = c_1 A/a$. Further simplifying, we have that

$$\begin{aligned} (a^2 - A^2) \sin(AL) &= -2aA \cos(AL) \\ \tan(AL) &= \frac{-2aA}{a^2 - A^2} \\ \tan\left(aL\sqrt{R/\lambda - 1}\right) &= \frac{2\lambda\sqrt{R/\lambda - 1}}{R} \end{aligned} \quad (2.18)$$

which we can use to numerically determine the principal eigenvalue. For example, Figure 2.1 plots the two functions $g(\lambda) = \tan(aL\sqrt{R/\lambda - 1})$ and $h(\lambda) = (2\lambda\sqrt{R/\lambda - 1})/R$ for $a = 1$, $R = 2$, and $L = 5$. The principal eigenvalue is the largest intersection of the functions, except for the intersection at $(R, 0)$, since this corresponds to $\lambda = R$, but we required $\lambda < R$ to obtain Equation 2.18. In this case, $\lambda_1 \approx 1.24 > 1$, so the population will persist. In contrast, for $L = 3$ we have $\lambda_1 \approx .74 < 1$, so the population will die out. This demonstrates how the eigenvalue analysis developed for the time-independent model can yield important information about the persistence of a population.

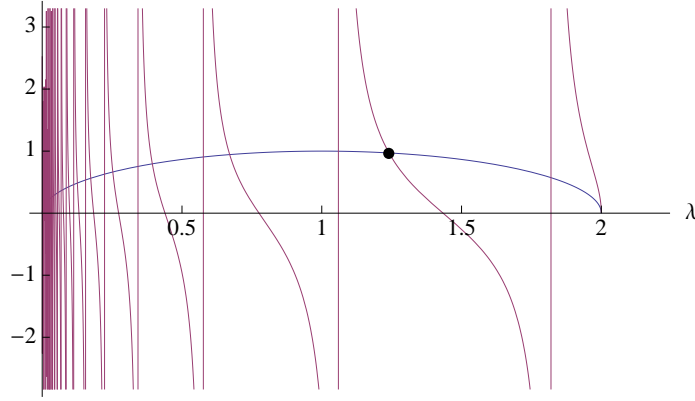


Figure 2.1 Plot of $g(\lambda) = \tan(aL\sqrt{R/\lambda-1})$ (in pink) and $h(\lambda) = (2\lambda\sqrt{R/\lambda-1})/R$ (in blue) for $a = 1$, $R = 2$, and $L = 5$. The principal eigenvalue is the largest value at which the curves cross (indicated by the point), except when they meet at $(R, 0)$. For these values, $\lambda_1 \approx 1.24 > 1$, indicating survival.

2.2 Time-Dependent Model

A more realistic model of population growth does not assume that the growth function f and dispersal kernel K remain constant at each time step. If we want to include temporal variation in our model, we can replace Equation 2.1 with the generalized model

$$n_{t+1}(x) = \int_{\Omega} K_t(x, y) f_t(n_t(y)) dy \quad (2.19)$$

where f_t and K_t are the growth function and dispersal kernel for the t^{th} time period. Thus we have that

$$n_{t+1}(x) = F_t[n_t](x)$$

where F_t is the time-varying Hammerstein operator defined by

$$F_t[n](x) = \int_{\Omega} K_t(x, y) f_t(n(y)) dy.$$

We can now define \mathcal{L}_t to be the linearization of F_t around the zero solution, so that

$$\mathcal{L}_t n_t(x) = R_t \int_{\Omega} K_t(x, y) n_t(y) dy$$

where $R_t = f'_t(0)$. Although this all seems analogous to the time-independent case, because the linearization varies at each time step, we cannot find a principal eigenvalue that will determine the behavior of the system. However, Hardin et al. (1988) have shown that we can understand the asymptotic growth rate of the system through the limit

$$r = \lim_{t \rightarrow \infty} \|\mathcal{L}_t \circ \cdots \circ \mathcal{L}_2 \circ \mathcal{L}_1\|^{1/t} \quad (2.20)$$

which replaces the notion of the principal eigenvalue. That is, if $r < 1$ it implies asymptotic stability of the zero solution and extinction, and if $r > 1$ it implies instability and persistence.

Let us define the *effective eigenvalue* to be

$$\Lambda = \lim_{t \rightarrow \infty} \left[\int_{\Omega} n_t(x) dx \right]^{1/t} \quad (2.21)$$

where here $n_t(x) = \mathcal{L}_t \circ \cdots \circ \mathcal{L}_2 \circ \mathcal{L}_1 n_0(x)$. Our first result is to prove an inequality for the time-dependent model which is analogous to that given in Equation 2.10 for the time-independent case.

Theorem 2.1. *For Λ and r defined above, we have that*

$$\Lambda \leq r. \quad (2.22)$$

Proof. First, let

$$\Lambda_t = \left(\int_{\Omega} n_t(x) dx \right)^{1/t}$$

and

$$r_t = \|\mathcal{L}_t \circ \cdots \circ \mathcal{L}_2 \circ \mathcal{L}_1\|^{1/t}$$

where $\|\cdot\|$ is the operator norm. Then we have

$$\begin{aligned} \Lambda_t &= \left(\int_{\Omega} n_t(x) dx \right)^{1/t} \\ &\leq \left(\int_{\Omega} \|n_t(x)\|_{\infty} dx \right)^{1/t} \\ &\leq |\Omega|^{1/t} \|n_t\|_{\infty}^{1/t}. \end{aligned} \quad (2.23)$$

Notice that it follows from the definition of the operator norm that

$$\|T\| \geq \|T(u/\|u\|_{\infty})\|_{\infty} = \frac{\|Tu\|_{\infty}}{\|u\|_{\infty}}$$

for any linear operator T and for all $u \in C(\overline{\Omega})$. Thus $\|Tu\|_\infty \leq \|T\| \|u\|_\infty$ for all u . Specifically, for the linear operator $\mathcal{L}_t \circ \cdots \circ \mathcal{L}_2 \circ \mathcal{L}_1$ and the function n_0 , we have

$$\|\mathcal{L}_t \circ \cdots \circ \mathcal{L}_2 \circ \mathcal{L}_1 n_0\|_\infty = \|n_t\|_\infty \leq \|\mathcal{L}_t \circ \cdots \circ \mathcal{L}_2 \circ \mathcal{L}_1\| \|n_0\|_\infty$$

which, combined with Equation 2.23, yields

$$\begin{aligned} \Lambda_t &\leq |\Omega|^{1/t} \|n_0\|_\infty^{1/t} \|\mathcal{L}_t \circ \cdots \circ \mathcal{L}_2 \circ \mathcal{L}_1\|^{1/t} \\ \Lambda_t &\leq |\Omega|^{1/t} \|n_0\|_\infty^{1/t} r_t. \end{aligned} \tag{2.24}$$

In the trivial case when $n_0(x) = 0$, we know the theorem must hold, since we will have $\Lambda = 0$ and $r \geq 0$. Then for nontrivial initial population densities, both $|\Omega|$ and $\|n_0\|_\infty$ are nonzero and finite (recall that we have a bounded domain). Thus if we take the limit of Equation 2.24 as t goes to infinity, we get that

$$\Lambda = \lim_{t \rightarrow \infty} \Lambda_t \leq \lim_{t \rightarrow \infty} |\Omega|^{1/t} \|n_0\|_\infty^{1/t} r_t = r$$

since $|\Omega|^{1/t} \rightarrow 1$ and $\|n_0\|_\infty^{1/t} \rightarrow 1$ as $t \rightarrow \infty$, completing the proof of the theorem. \square

This result is useful because the operator norm in r is in general difficult to calculate, but the integral in Λ may be much easier to compute or approximate, especially in a random setting. Since $\Lambda > 1$ implies $r > 1$, it is sufficient to ensure that $\Lambda > 1$ to guarantee survival of a population in a time-dependent model.

Chapter 3

Alternating Laplace Kernels

3.1 Laplace Kernels

The dispersal kernel $K(x, y)$ describes the way in which individuals in a population spread out during the dispersal stage. For example, if a population moves randomly with diffusion coefficient D for a fixed period of time T , then the dispersal kernel will be a Gaussian of the form

$$K(x, y) = \frac{1}{\sqrt{4\pi DT}} e^{-(x-y)^2/4DT}$$

as shown in Neubert et al. (1995). On the other hand, if randomly moving individuals do not settle simultaneously after a fixed time period, but instead settle at a constant rate α , then the resulting dispersal kernel is the symmetric Laplace kernel

$$K(x, y) = \sqrt{\frac{\alpha}{4D}} e^{-\sqrt{\alpha/D}|x-y|}$$

described in Section 2.1.1. Furthermore, if the population is subjected to a unidirectional flow of velocity v , such as in a river or wind environment, then Lutscher et al. (2005) show that the dispersal kernel satisfies the differential equation

$$\frac{D}{\alpha} K_{xx} - \frac{v}{\alpha} K_x - K = -\delta(x - y). \quad (3.1)$$

We also require that the probability that an individual settles at x approaches zero as $x \rightarrow \infty$ and that K approaches the same value coming from the left

or the right of the starting position y . Applying these boundary conditions to Equation 3.1, the dispersal kernel takes the form of an asymmetric Laplace kernel given by

$$K(x, y) = \begin{cases} Ae^{a(x-y)} & x < y \\ Ae^{b(x-y)} & x \geq y \end{cases} \quad (3.2)$$

where

$$a = \frac{v}{2D} + \sqrt{\frac{v^2}{4D^2} + \frac{\alpha}{D}}, \quad (3.3)$$

$$b = \frac{v}{2D} - \sqrt{\frac{v^2}{4D^2} + \frac{\alpha}{D}}, \quad (3.4)$$

and

$$A = \frac{ab}{b-a} \quad (3.5)$$

(Lutscher et al., 2005). It is easy to see that if $v = 0$ in the above equations, then this kernel reduces to the symmetric Laplace kernel and is therefore a generalization of Equation 2.13. This model is very useful for describing the dispersal behavior of many species living in habitats that may be influenced by a unidirectional flow, and it will therefore be the primary model of dispersal we consider.

3.2 Two-Step Kernel

Jacobsen et al. (2013) consider a time-dependent model in which a species disperses in two alternating stages, each with its own known dispersal kernel and linearized growth rate. Such a model could represent a species that disperses in two different seasons that affect dispersal behavior in a predictable way, for example, a river population that disperses once in the summer, when the flow velocity is low, and once in the winter, when flow velocity is high.

In the linearization of this two-step model, the population density (near zero) after the first dispersal stage is given by

$$n_{t+1}(x) = R_1 \int_{\Omega} K_1(x, y) n_t(y) dy$$

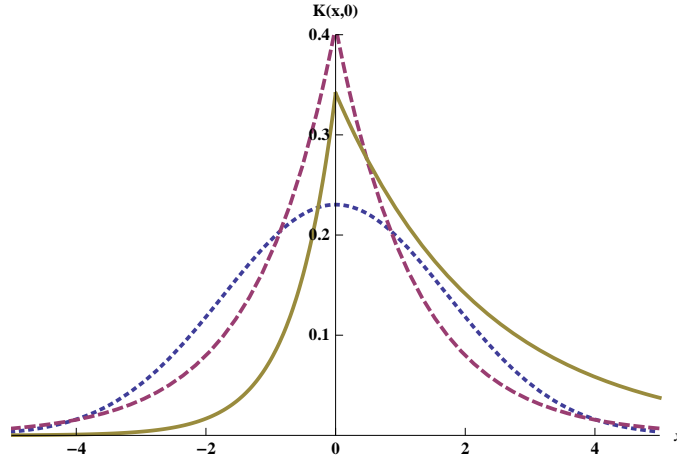


Figure 3.1 A Gaussian kernel (dotted), symmetric Laplace kernel (dashed), and asymmetric Laplace kernel (solid) at $y = 0$.

and after the second stage we have that

$$n_{t+2}(x) = R_2 \int_{\Omega} K_2(x, y) n_{t+1}(y) dy.$$

Combining these two stages, we get

$$\begin{aligned} n_{t+2}(x) &= R_2 \int_{\Omega} K_2(x, y) n_{t+1}(y) dy \\ &= R_2 \int_{\Omega} K_2(x, y) \left[R_1 \int_{\Omega} K_1(y, z) n_t(z) dz \right] dy \\ &= R_1 R_2 \int_{\Omega} \int_{\Omega} K_2(x, y) K_1(y, z) n_t(z) dz dy \end{aligned}$$

which we can represent as a single, linearized, time-invariant integrodifference equation that effectively models both stages with one growth rate and one dispersal kernel:

$$n_{t+1}(x) = R \int_{\Omega} K(x, z) n_t(z) dz \quad (3.6)$$

where $R = R_1 R_2$, the effective dispersal kernel is

$$K(x, z) = \int_{\Omega} K_2(x, y) K_1(y, z) dy, \quad (3.7)$$

and each time step in this new equation represents two stages in the original system. Since this combined model gives the population density after

every other time step in the original two-step model, the long-term dynamics will be the same.

By Equation 2.8, we know that the principal eigenvalue of this combined model satisfies $\lambda_1 \leq R_1 R_2$. Since this represents the population growth after two time steps, the effective principal eigenvalue for one time step in the original model is $\lambda'_1 = \sqrt{\lambda_1} \leq \sqrt{R_1 R_2}$. In particular, if $\lambda_1 > 1$, then $\lambda'_1 > 1$, indicating persistence for the population, and if $\lambda_1 < 1$, then $\lambda'_1 < 1$, indicating extinction.

To determine the principal eigenvalue of Equation 3.6, we examine the eigenvalue equation

$$R \int_{\Omega} K(x, z) \phi(z) dz = R_1 R_2 \int_{\Omega} \int_{\Omega} K_2(x, y) K_1(y, z) \phi(z) dz dy = \lambda \phi(x). \quad (3.8)$$

If we define

$$\psi(x) = R_1 \int_{\Omega} K_1(x, y) \phi(y) dy \quad (3.9)$$

then we see from Equation 3.8 that

$$\phi(x) = \frac{R_2}{\lambda} \int_{\Omega} K_2(x, y) \psi(y) dy. \quad (3.10)$$

Now suppose we have a population on $\Omega = (0, L)$ that disperses according to an asymmetric Laplace kernel in both stages, so that K_1 has parameters α_1 , D_1 , and v_1 , and K_2 has parameters α_2 , D_2 , and v_2 . By differentiating Equation 3.9 twice and using Equation 3.1, we see that

$$\begin{aligned} \psi''(x) &= R_1 \int_{\Omega} K_{1xx}(x, y) \phi(y) dy \\ &= R_1 \int_{\Omega} \left[\frac{v_1}{D_1} K_{1x}(x, y) + \frac{\alpha_1}{D_1} K(x, y) - \frac{\alpha_1}{D_1} \delta(x - y) \right] \phi(y) dy \\ &= \frac{v_1}{D_1} \psi'(x) + \frac{\alpha_1}{D_1} \psi(x) - \frac{\alpha_1 R_1}{D_1} \int_{\Omega} \delta(x - y) \phi(y) dy \\ &= \frac{v_1}{D_1} \psi'(x) + \frac{\alpha_1}{D_1} \psi(x) - \frac{\alpha_1 R_1}{D_1} \phi(x). \end{aligned} \quad (3.11)$$

Repeating this process on Equation 3.10 gives us that

$$\phi''(x) = \frac{v_2}{D_2} \phi'(x) + \frac{\alpha_2}{D_2} \phi(x) - \frac{\alpha_2 R_2}{\lambda D_2} \psi(x). \quad (3.12)$$

Now, if we differentiate Equation 3.12 twice and substitute Equation 3.11 for $\psi''(x)$, we have

$$\phi^{(4)} = \frac{v_2}{D_2}\phi^{(3)} + \frac{\alpha_2}{D_2}\phi'' - \frac{\alpha_2 R_2}{\lambda D_2} \left(\frac{v_1}{D_1}\psi' + \frac{\alpha_1}{D_1}\psi - \frac{\alpha_1 R_1}{D_1}\phi \right). \quad (3.13)$$

Finally, from Equation 3.12 we know that

$$\frac{\alpha_2 R_2}{\lambda D_2}\psi(x) = \phi''(x) - \frac{v_2}{D_2}\phi'(x) - \frac{\alpha_2}{D_2}\phi(x), \quad (3.14)$$

so substituting this and its derivative in for ψ and ψ' in Equation 3.13 above, we derive the following fourth-order ordinary differential equation for the two-step eigenfunction:

$$\phi^{(4)} = C_3\phi^{(3)} + C_2\phi'' + C_1\phi' + C_0\phi \quad (3.15)$$

where

$$\begin{aligned} C_3 &= \frac{v_1}{D_1} + \frac{v_2}{D_2} \\ C_2 &= \frac{\alpha_1}{D_1} + \frac{\alpha_2}{D_2} - \frac{v_1 v_2}{D_1 D_2} \\ C_1 &= -\frac{v_1 \alpha_2}{D_1 D_2} - \frac{v_2 \alpha_1}{D_1 D_2} \\ \text{and } C_0 &= -\frac{\alpha_1 \alpha_2}{D_1 D_2} + \frac{\alpha_1 \alpha_2 R_1 R_2}{\lambda D_1 D_2} \end{aligned}$$

(Jacobsen et al., 2013). Since this is a constant-coefficient, linear, ordinary differential equation, the general solution is

$$\phi(x) = b_1 e^{r_1 x} + b_2 e^{r_2 x} + b_3 e^{r_3 x} + b_4 e^{r_4 x}$$

where the r_i are the roots of the characteristic equation. The precise eigenfunctions are determined by the boundary conditions.

To derive boundary conditions for Equation 3.15, we first notice that by Equation 3.2 the dispersal kernel K_2 is

$$K_2(x, y) = \begin{cases} A_2 e^{a_2(x-y)} & x < y \\ A_2 e^{b_2(x-y)} & x \geq y \end{cases}$$

where a_2 and b_2 are given by Equations 3.3 and 3.4 and A_2 is given by Equation 3.5 with parameters α_2 , D_2 , and v_2 . Substituting this into Equation 3.10, we get

$$\phi(x) = \frac{R_2}{\lambda} \left(\int_x^L A_2 e^{a_2(x-y)} \psi(y) dy + \int_0^x A_2 e^{b_2(x-y)} \psi(y) dy \right) \quad (3.16)$$

which, at $x = 0$, is

$$\phi(0) = \frac{R_2}{\lambda} \int_0^L A_2 e^{-a_2 y} \psi(y) dy. \quad (3.17)$$

Then, taking the derivative of ϕ in Equation 3.16, we see that

$$\phi'(x) = \frac{R_2}{\lambda} \left(\int_x^L A_2 a_2 e^{a_2(x-y)} \psi(y) dy + \int_0^x A_2 b_2 e^{b_2(x-y)} \psi(y) dy \right) \quad (3.18)$$

which, at $x = 0$, is

$$\phi'(0) = a_2 \frac{R_2}{\lambda} \int_0^L A_2 e^{-a_2 y} \psi(y) dy. \quad (3.19)$$

Thus, we see that

$$\phi'(0) = a_2 \phi(0). \quad (3.20)$$

Using the same method as above, but instead substituting $x = L$ into Equations 3.16 and 3.18, we may derive that

$$\phi'(L) = b_2 \phi(L). \quad (3.21)$$

Similarly, from Equation 3.9 we derive that $\psi'(0) = a_1 \psi(0)$ and $\psi'(L) = b_1 \psi(L)$. To convert these last two boundary conditions into equations in terms of ϕ , we again use Equation 3.14 to replace ψ and ψ' with derivatives of ϕ , evaluated at $x = 0$ and $x = L$. After collecting terms, we get the boundary conditions:

$$\phi^{(3)}(0) = \left(a_1 + \frac{v_2}{D_2} \right) \phi''(0) + \left(\frac{\alpha_2}{D_2} - \frac{a_1 v_2}{D_2} \right) \phi'(0) - \frac{a_1 \alpha_2}{D_2} \phi(0) \quad (3.22)$$

$$\phi^{(3)}(L) = \left(b_1 + \frac{v_2}{D_2} \right) \phi''(L) + \left(\frac{\alpha_2}{D_2} - \frac{b_1 v_2}{D_2} \right) \phi'(L) - \frac{b_1 \alpha_2}{D_2} \phi(L) \quad (3.23)$$

(Jacobsen et al., 2013).

The differential equation given by Equation 3.15, along with the boundary conditions in Equations 3.20–3.23 form a boundary value problem that can be used to numerically approximate or analytically solve for the principal eigenvalue λ_1 of the combined model or the effective principal eigenvalue $\lambda'_1 = \sqrt{\lambda_1}$ for a single time step in the original model (Jacobsen et al., 2013). For example, Figure 3.2 plots λ'_1 as a function of the domain length L for given fixed parameters of K_1 and K_2 . For these parameters, the critical domain length is $L \approx 4.425$.

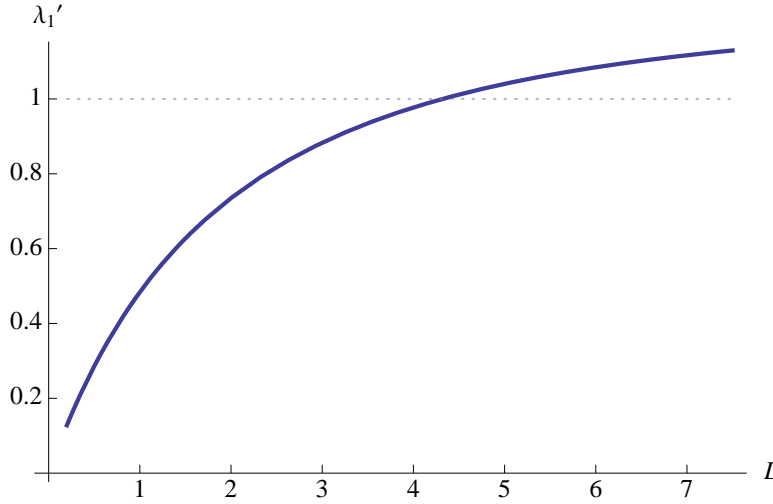


Figure 3.2 The effective principal eigenvalue $\lambda_1' = \sqrt{\lambda_1}$ for the two-step model with $\alpha_1 = \alpha_2 = D_1 = D_2 = 1$, $v_1 = 0.1$, $v_2 = 1$, $R_1 = 1.2$, and $R_2 = 1.5$ (solved numerically in Mathematica).

3.3 N-Step Kernel

The natural question to ask now is: Can the two-step model be extended to an N -step model of N alternating Laplace kernels? In fact, we will show that it is always possible to combine N alternating kernels into a single one-step model. Furthermore, if the kernels are Laplace kernels, it is possible to derive a $2N^{\text{th}}$ -order, linear, constant-coefficient, ordinary differential equation and $2N$ boundary conditions that allow us to solve for the eigenfunctions and eigenvalues of the linear operator for the combined model, as was done in the case of the two-step model. Thus we may determine the conditions for survival for a wide range of populations that disperse in multiple stages, such as a variety of woody plants that have been shown to disperse according to alternating supra-annual schedules (Herrera et al., 1998).

Suppose we have a population that disperses in N alternating stages, with dispersal kernels K_1, K_2, \dots, K_N and corresponding linearized growth rates R_1, R_2, \dots, R_N . Then inductively we see that the population density

(near zero) after the $(t + N)^{\text{th}}$ stage is

$$\begin{aligned}
 n_{t+N}(x) &= R_N \int_{\Omega} K_N(x, x_N) n_{t+N-1}(x_N) dx_N \\
 &= R_N R_{N-1} \int_{\Omega} \int_{\Omega} K_N(x, x_N) K_{N-1}(x_N, x_{N-1}) n_{t+N-2}(x_{N-1}) dx_N dx_{N-1} \\
 &\quad \vdots \\
 &= \prod_{i=1}^N R_i \int_{\Omega} \cdots \int_{\Omega} \left(\prod_{i=1}^N K_i(x_{i+1}, x_i) \right) n_t(x_1) dx_N \cdots dx_1
 \end{aligned} \tag{3.24}$$

where we have let $x = x_{N+1}$ for convenience. We can represent Equation 3.24 as a single, linearized, time-invariant integrodifference equation of the form

$$n_{t+1}(x) = R \int_{\Omega} K(x, x_1) n_t(x_1) dx_1 \tag{3.25}$$

where $R = \prod_{i=1}^N R_i$ and

$$K(x, x_1) = \int_{\Omega} \cdots \int_{\Omega} \prod_{i=1}^N K_i(x_{i+1}, x_i) dx_N \cdots dx_2 \tag{3.26}$$

is the combined dispersal kernel. Every time step in this model represents N stages in the original model.

Since the principal eigenvalue λ_1 for the combined system, λ_1 , corresponds to N periods of growth, the principal eigenvalue for one time step in the original model is effectively $\lambda'_1 = \lambda_1^{1/N}$. As before, $\lambda_1 > 1$ implies $\lambda'_1 > 1$ and $\lambda_1 < 1$ implies $\lambda'_1 < 1$, so the conditions for persistence are the same for the combined equation as they are in the original model, as we expect. In addition, by Equation 2.8, we know that λ'_1 is bounded by $(R_1 R_2 \cdots R_N)^{1/N}$, the geometric mean of the individual linearized growth rates.

Now consider the eigenvalue equation for the combined model:

$$R \int_{\Omega} K(x, y) \phi_N(y) dy = \lambda \phi_N(x). \tag{3.27}$$

If we define

$$\begin{aligned}
 \phi_1(x) &= R_1 \int_{\Omega} K_1(x, y) \phi_N(y) dy \\
 \phi_2(x) &= R_2 \int_{\Omega} K_2(x, y) \phi_1(y) dy \\
 &\vdots \\
 \phi_{N-1}(x) &= R_{N-1} \int_{\Omega} K_{N-1}(x, y) \phi_{N-2}(y) dy
 \end{aligned} \tag{3.28}$$

then (recalling the definition of R and K) we see that $\phi_N(x)$ solves Equation 3.27 if and only if

$$\phi_N(x) = \frac{R_N}{\lambda} \int_{\Omega} K_N(x, y) \phi_{N-1}(y) dy. \tag{3.29}$$

Now assume that each dispersal kernel K_i is an asymmetric Laplace kernel with parameters α_i , D_i , and v_i and corresponding a_i and b_i given by Equations 3.3 and 3.4. Then as we did for the two-step model, we can differentiate each of the equations in 3.28 twice and substitute in the differential equation from 3.1 for each K_i to get the system of ordinary differential equations:

$$\begin{aligned}
 \phi_1''(x) &= \frac{v_1}{D_1} \phi_1'(x) + \frac{\alpha_1}{D_1} \phi_1(x) - \frac{\alpha_1 R_1}{D_1} \phi_N(x) \\
 \phi_2''(x) &= \frac{v_2}{D_2} \phi_2'(x) + \frac{\alpha_2}{D_2} \phi_2(x) - \frac{\alpha_2 R_2}{D_2} \phi_1(x) \\
 \phi_3''(x) &= \frac{v_3}{D_3} \phi_3'(x) + \frac{\alpha_3}{D_3} \phi_3(x) - \frac{\alpha_3 R_3}{D_3} \phi_2(x) \\
 &\vdots \\
 \phi_N''(x) &= \frac{v_N}{D_N} \phi_N'(x) + \frac{\alpha_N}{D_N} \phi_N(x) - \frac{\alpha_N R_N}{\lambda D_N} \phi_{N-1}(x).
 \end{aligned} \tag{3.30}$$

To combine these equations into a single differential equation for the eigenfunction ϕ_N we will need the following lemma.

Lemma 3.1. *For the system of ordinary differential equations*

$$\begin{aligned}
 \phi_1''(x) &= c_{1,1} \phi_1'(x) + c_{1,2} \phi_1(x) + c_{1,3} \phi_0(x) \\
 \phi_2''(x) &= c_{2,1} \phi_2'(x) + c_{2,2} \phi_2(x) + c_{2,3} \phi_1(x) \\
 &\vdots \\
 \phi_N''(x) &= c_{N,1} \phi_N'(x) + c_{N,2} \phi_N(x) + c_{N,3} \phi_{N-1}(x)
 \end{aligned}$$

we have that

$$0 = \sum_{k=0}^{2N} C(N, k) \phi_N^{(2N-k)} - \left(\prod_{k=1}^N c_{k,3} \right) \phi_0 \quad (3.31)$$

where $C(N, k)$ is the sum of all products of the coefficients $c_{i,1}$ and $c_{i,2}$ ($1 \leq i \leq N$) in the system above such that the second indices sum to k and no two first indices are equal, and where terms with an odd number of coefficients being multiplied are negated.

Before presenting the proof of the lemma, let us first give an example and a brief remark to help elucidate the meaning of $C(N, k)$.

Example. When $N = 3$, we have the system of equations

$$\begin{aligned} \phi_1''(x) &= c_{1,1}\phi_1'(x) + c_{1,2}\phi_1(x) + c_{1,3}\phi_0(x) \\ \phi_2''(x) &= c_{2,1}\phi_2'(x) + c_{2,2}\phi_2(x) + c_{2,3}\phi_1(x) \\ \phi_3''(x) &= c_{3,1}\phi_3'(x) + c_{3,2}\phi_3(x) + c_{3,3}\phi_2(x). \end{aligned} \quad (3.32)$$

According to the lemma, the resulting equation we get from this system is

$$\begin{aligned} 0 &= \phi_3^{(6)} \\ &+ (-c_{1,1} - c_{2,1} - c_{3,1})\phi_3^{(5)} \\ &+ (-c_{1,2} - c_{2,2} - c_{3,2} + c_{1,1}c_{2,1} + c_{1,1}c_{3,1} + c_{2,1}c_{3,1})\phi_3^{(4)} \\ &+ (c_{1,1}c_{2,2} + c_{1,1}c_{3,2} + c_{1,2}c_{2,1} + c_{2,1}c_{3,2} + c_{1,2}c_{3,1} + c_{2,2}c_{3,1} - c_{1,1}c_{2,1}c_{3,1})\phi_3^{(3)} \\ &+ (c_{1,2}c_{2,2} + c_{1,2}c_{3,2} + c_{2,2}c_{3,2} - c_{1,1}c_{2,1}c_{3,2} - c_{1,1}c_{2,2}c_{3,1} - c_{1,2}c_{2,1}c_{3,1})\phi_3'' \\ &+ (-c_{1,1}c_{2,2}c_{3,2} - c_{1,2}c_{2,1}c_{3,2} - c_{1,2}c_{2,2}c_{3,1})\phi_3' \\ &+ (-c_{1,2}c_{2,2}c_{3,2})\phi_3 \\ &- c_{1,3}c_{2,3}c_{3,3}\phi_0. \end{aligned}$$

Notice, for example, how the coefficient in front of $\phi_3^{(4)}$ consists of a sum of all products of coefficients in Equation 3.32 with second index 1 or 2 such that the second indices sum to 2 (since $4 = 2N - 2$) and no two first indices are the same. Notice also how all terms with an odd number of coefficients are negative. This demonstrates the precise meaning of the lemma above.

Remark. With a few definitions, we may provide a closed form for the coefficients $C(N, k)$. Let

$$\mathcal{S}_N = \bigoplus_{i=1}^N \mathbb{Z}_3$$

be the set of N -tuples of elements from $\mathbb{Z}_3 = \{0, 1, 2\}$ and let s_i be the i^{th} entry of $s \in \mathcal{S}_N$. Furthermore, let

$$\mathcal{S}_{N,k} = \left\{ s \in \mathcal{S}_N \left| \sum_{i=1}^N s_i = k \right. \right\}$$

be the set of elements in \mathcal{S}_N such that the entries sum to k . Define the parity $\sigma(s)$ of $s \in \mathcal{S}_N$ to be the number of nonzero entries s_i in s . Then based on the definition given in Lemma 3.1, we have that

$$C(N, k) = \sum_{s \in \mathcal{S}_{N,k}} (-1)^{\sigma(s)} \prod_{i=1}^N c_{i,s_i} \quad (3.33)$$

where $c_{i,0} = 1$ for all i . This provides a closed form for the coefficients as well as a potential way of computing them.

Notice that by this definition, we have $C(N, 0) = 1$ (since we have only one term in our series and it consists of the empty product) and $C(N, k) = 0$ for $k < 0$ or $k > 2N$ (since for these values we have an empty sum). This makes sense by our previous definition because there are no ways to multiply the $c_{i,1}$ and $c_{i,2}$ so that the sum of the indices is less than zero or greater than $2N$ and no two first indices are the same.

The proof of the lemma is as follows.

Proof of Lemma 3.1. We will proceed by induction on N . For $N = 1$, our system is just

$$\begin{aligned} \phi_1''(x) &= c_{1,1}\phi_1'(x) + c_{2,1}\phi_1(x) + c_{3,1}\phi_0(x) \\ 0 &= \phi_1''(x) - c_{1,1}\phi_1'(x) - c_{2,1}\phi_1(x) - c_{3,1}\phi_0(x) \end{aligned}$$

which is already in the form provided by the lemma.

Suppose the lemma holds for the case of N . In the $N + 1$ case, we have the system of differential equations:

$$\phi_1''(x) = c_{1,1}\phi_1'(x) + c_{1,2}\phi_1(x) + c_{1,3}\phi_0(x) \quad (3.34)$$

$$\phi_2''(x) = c_{2,1}\phi_2'(x) + c_{2,2}\phi_2(x) + c_{2,3}\phi_1(x) \quad (3.35)$$

\vdots

$$\phi_N''(x) = c_{N,1}\phi_N'(x) + c_{N,2}\phi_N(x) + c_{N,3}\phi_{N-1}(x) \quad (3.36)$$

$$\phi_{N+1}''(x) = c_{N+1,1}\phi_{N+1}'(x) + c_{N+1,2}\phi_{N+1}(x) + c_{N+1,3}\phi_N(x). \quad (3.37)$$

Since the first N equations satisfy the conditions of the lemma, by our induction hypothesis we have an equation for $\phi_N^{(2N)}$:

$$\phi_N^{(2N)} = - \sum_{k=1}^{2N} C(N, k) \phi_N^{(2N-k)} + \left(\prod_{k=1}^N c_{k,3} \right) \phi_0.$$

Thus we can take $2N$ derivatives of Equation 3.37 and substitute in for $\phi_N^{(2N)}$ to get

$$\begin{aligned} \phi_{N+1}^{(2N+2)} &= c_{N+1,1} \phi_{N+1}^{(2N+1)} + c_{N+1,2} \phi_{N+1}^{(2N)} \\ &\quad - c_{N+1,3} \left[\sum_{k=1}^{2N} C(N, k) \phi_N^{(2N-k)} + \left(\prod_{k=1}^N c_{k,3} \right) \phi_0 \right] \end{aligned}$$

which we can rewrite as

$$\begin{aligned} \phi_{N+1}^{(2N+2)} &= c_{N+1,1} \phi_{N+1}^{(2N+1)} + c_{N+1,2} \phi_{N+1}^{(2N)} \\ &\quad - \sum_{k=1}^{2N} C(N, k) c_{N+1,3} \phi_N^{(2N-k)} + \left(\prod_{k=1}^{N+1} c_{k,3} \right) \phi_0. \end{aligned}$$

Now, since we know $c_{N+1,3} \phi_N = \phi_{N+1}'' - c_{N+1,1} \phi_{N+1}' - c_{N+1,2} \phi_{N+1}$ from Equation 3.37, we can replace all derivatives the ϕ_N in the above sum with derivatives of ϕ_{N+1} , giving

$$\begin{aligned} \phi_{N+1}^{(2N+2)} &= c_{N+1,1} \phi_{N+1}^{(2N+1)} + c_{N+1,2} \phi_{N+1}^{(2N)} \\ &\quad - \sum_{k=1}^{2N} C(N, k) \left(\phi_{N+1}^{(2N+2-k)} - c_{N+1,1} \phi_{N+1}^{(2N+1-k)} - c_{N+1,2} \phi_{N+1}^{(2N-k)} \right) \\ &\quad + \left(\prod_{k=1}^{N+1} c_{k,3} \right) \phi_0 \end{aligned}$$

which, by distributing the sum and reindexing, can be written as

$$\begin{aligned} \phi_{N+1}^{(2N+2)} &= c_{N+1,1} \phi_{N+1}^{(2N+1)} + c_{N+1,2} \phi_{N+1}^{(2N)} \\ &\quad - \sum_{k=1}^{2N} C(N, k) \phi_{N+1}^{(2N+2-k)} + \sum_{k=2}^{2N+1} c_{N+1,1} C(N, k-1) \phi_{N+1}^{(2N+2-k)} \\ &\quad + \sum_{k=3}^{2N+2} c_{N+1,2} C(N, k-2) \phi_{N+1}^{(2N+2-k)} + \left(\prod_{k=1}^{N+1} c_{k,3} \right) \phi_0. \end{aligned}$$

Recall from our Remark that $C(N, k) = 0$ for $k < 0$ or $k > 2N$ and $C(N, 0) = 1$. Thus we may write

$$\begin{aligned} 0 &= C(N, 0)\phi_{N+1}^{(2N+2)} - c_{N+1,1}C(N, 0)\phi_{N+1}^{(2N+1)} - c_{N+1,2}C(N, 0)\phi_{N+1}^{(2N)} \\ &\quad + \sum_{k=1}^{2N+2} C(N, k)\phi_{N+1}^{(2N+2-k)} - \sum_{k=2}^{2N+2} c_{N+1,1}C(N, k-1)\phi_{N+1}^{(2N+2-k)} \\ &\quad - \sum_{k=3}^{2N+2} c_{N+1,2}C(N, k-2)\phi_{N+1}^{(2N+2-k)} - \left(\prod_{k=1}^{N+1} c_{k,3}\right)\phi_0 \end{aligned}$$

which, after folding the first three terms into the appropriate sums and recalling that $C(N, k) = 0$ for $k < 0$, may finally be written as

$$\begin{aligned} 0 &= \sum_{k=0}^{2N+2} (C(N, k) - c_{N+1,1}C(N, k-1) - c_{N+1,2}C(N, k-2))\phi_{N+1}^{(2N+2-k)} \\ &\quad - \left(\prod_{k=1}^{N+1} c_{k,3}\right)\phi_0. \end{aligned} \tag{3.38}$$

To complete the proof, we show that

$$C(N+1, k) = C(N, k) - c_{N+1,1}C(N, k-1) - c_{N+1,2}C(N, k-2). \tag{3.39}$$

To see this, first notice that since no two first indices may be the same in any of the coefficients in a single term of $C(N+1, k)$, each term must contain either $c_{N+1,1}$ or $c_{N+1,2}$ or no coefficient with first index $N+1$. All possible terms that do not contain such a coefficient must be products of coefficients of the first N equations such that the second indices sum to k and terms with an even number of coefficients are negated, the sum of which is by definition $C(N, k)$. Furthermore, any term in $C(N+1, k)$ with $c_{N+1,1}$ in it will be $c_{N+1,1}$ times a product of coefficients of the first N equations such that the second indices sum to $k-1$, guaranteeing that the total sum of the second indices is k . Then, since multiplying by $c_{N+1,1}$ changes the number of coefficients in the product from odd to even or even to odd, the sum of all terms in $C(N+1, k)$ containing $c_{N+1,1}$ is $-c_{N+1,1}C(N, k-1)$. Similarly, any term in $C(N+1, k)$ with $c_{N+1,2}$ in it will be $c_{N+1,2}$ times a product of coefficients of the first N equations such that the second indices sum to $k-2$, and multiplying by $c_{N+1,2}$ changes the parity, so the sum of all terms in $C(N+1, k)$ containing $c_{N+1,2}$ is $-c_{N+1,2}C(N, k-2)$. Therefore $C(N+1, k)$ is the sum of these three collections of terms, as stated in Equation 3.39.

Thus Equation 3.38 becomes

$$0 = \sum_{k=0}^{2N+2} C(N+1, k) \phi_{N+1}^{(2N+2-k)} - \left(\prod_{k=1}^{N+1} c_{k,3} \right) \phi_0 \quad (3.40)$$

which satisfies Equation 3.31, completing our proof by induction. \square

Lemma 3.1 is significant to our problem of the N -step alternating kernel because it applies to the system of differential equations in 3.30 where $c_{i,1} = v_i/D_i$ and $c_{i,2} = \alpha_i/D_i$ for $i = 1, \dots, N$, $c_{i,3} = -\alpha_i R_i/D_i$ for $i = 1, \dots, N-1$, and $c_{N,3} = -\alpha_N R_N/\lambda D_N$, and where $\phi_0 = \phi_N$. Furthermore, since $\phi_0 = \phi_N$, the resulting equation is a $2N^{\text{th}}$ -order differential equation solely given in terms of ϕ_N . The fourth-order differential equation in 3.15 derived for the two-step model is an example of such a solution.

Now that we have a $2N^{\text{th}}$ -order differential equation for the N -step model, we want to find boundary conditions that let us solve for the eigenvalues and eigenfunctions of the associated linear operator for the combined model.

If the domain is $\Omega = (0, L)$, then we can use the definition of $K_i(x, y)$ in the equations in 3.28 and their derivatives evaluated at 0 and L as we did in the case of the two-step model to derive the set of boundary conditions:

$$\phi_i'(0) = a_i \phi_i(0) \quad (3.41)$$

$$\phi_i'(L) = b_i \phi_i(L) \quad (3.42)$$

for $i = 1, 2, \dots, N$. We can convert all of these boundary conditions into equations exclusively in terms of ϕ_N using the following lemma.

Lemma 3.2. *For the system of differential equations given in Lemma 3.1, if we have the boundary condition at $x = x_0$:*

$$\phi_i'(x_0) = m_i \phi_i(x_0)$$

for $i \in \{1, 2, \dots, N\}$, where m_i is a constant, then this leads to a boundary condition in terms of ϕ_N given by

$$0 = \sum_{k=0}^{2(N-i)+1} B_{m_i}(N, i, k) \phi_N^{(2(N-i)+1-k)}(x_0)$$

where $B_{m_i}(N, i, k)$ is the sum of all products of the coefficients $c_{j,1}$ and $c_{j,2}$ for $j = i+1, \dots, N$ and $m_i = m_{i,1}$ such that the second indices sum to k and no two first indices are equal, and where terms with an odd number of objects being multiplied are negated.

Example. Let $N = 3$. For $i = 1$, we get a fifth-order boundary condition

$$\begin{aligned}
 0 &= \phi_3^{(5)}(x_0) \\
 &+ (-m_{1,1} - c_{2,1} - c_{3,1})\phi_3^{(4)}(x_0) \\
 &+ (-c_{2,2} - c_{3,2} + m_{1,1}c_{2,1} + m_{1,1}c_{3,1} + c_{2,1}c_{3,1})\phi_3^{(3)}(x_0) \\
 &+ (m_{1,1}c_{2,2} + m_{1,1}c_{3,2} + c_{2,1}c_{3,2} + c_{2,2}c_{3,1} - m_{1,1}c_{2,1}c_{3,1})\phi_3''(x_0) \\
 &+ (c_{2,2}c_{3,2} - m_{1,1}c_{2,1}c_{3,2} - m_{1,1}c_{2,2}c_{3,1})\phi_3'(x_0) \\
 &+ (-m_{1,1}c_{2,2}c_{3,2})\phi_3(x_0)
 \end{aligned}$$

(recall that we let $m_i = m_{i,1}$ for clarity in the statement of the lemma). For $i = 2$, we get a third-order boundary condition

$$\begin{aligned}
 0 &= \phi_3^{(3)}(x_0) \\
 &+ (-m_{2,1} - c_{3,1})\phi_3''(x_0) \\
 &+ (-c_{3,2} + m_{2,1}c_{3,1})\phi_3'(x_0) \\
 &+ (m_{2,1}c_{3,2})\phi_3(x_0),
 \end{aligned}$$

and for $i = 3$ we simply get the original first-order boundary condition

$$\begin{aligned}
 \phi_3'(x_0) &= m_{3,1}\phi_3(x_0) \\
 0 &= \phi_3'(x_0) - m_{3,1}\phi_3(x_0)
 \end{aligned}$$

since there is only one term in the sum ($k = 1$) and the coefficient is just $B_{m_i}(3, 3, 1) = m_{3,1}$ since $j = 4, \dots, 3$ is vacuous.

Remark. As with $C(N, k)$, we can write $B_{m_i}(N, i, k)$ in a relatively simple closed form. Define $\mathcal{T}_{N,i}$ to be the set of $(N - i + 1)$ -tuples $(t_1, t_2, \dots, t_{N-i+1})$ where $t_1 \in \mathbb{Z}_2$ and $t_i \in \mathbb{Z}_3$ for $t_i = 2, 3, \dots, N - i + 1$. Define $\mathcal{T}_{N,i,k} \subset \mathcal{T}_{N,i}$ as the set of all $t \in \mathcal{T}_{N,i}$ such that the entries sum to k . Then

$$B_{m_i}(N, i, k) = \sum_{t \in \mathcal{T}_{N,i,k}} (-1)^{\sigma(t)} m_{i,1} \prod_{j=i+1}^N c_{i+j,t_j} \quad (3.43)$$

where the parity $\sigma(t)$ is defined as before and $c_{j,0} = 1$ for all j .

Notice that $B_{m_i}(N, i, 0) = 1$ (since we have a sum with only one term, consisting of the empty product) and that $B_{m_i}(N, i, k) = 0$ for $k < 0$ and $k > 2(N - i) + 1$ (since we have an empty sum for these values). Again, we see that this makes sense from our original definition of $B_{m_i}(N, i, k)$.

Proof of Lemma 3.2. As in the proof of Lemma 3.1, we will proceed by induction on N . For $N = 1$, the only possible boundary condition is

$$\phi_1'(x_0) = m_1\phi_1(x_0),$$

which is already in terms of ϕ_1 and satisfies the lemma.

Assume the lemma holds for N . Consider $N + 1$ differential equations of the form given in Lemma 3.1 with the boundary condition

$$\phi_i'(x_0) = m_i\phi_i(x_0).$$

If $i = N + 1$, then it is already in terms of $N + 1$ and satisfies the lemma. If $i < N + 1$, then it satisfies the conditions of the lemma for the first N differential equations, so we know by the induction hypothesis that we can write this in terms of ϕ_N as

$$0 = \sum_{k=0}^{2(N-i)+1} B_{m_i}(N, i, k) \phi_N^{(2(N-i)+1-k)}(x_0). \quad (3.44)$$

Recall that $c_{N+1,3}\phi_N(x) = \phi_{N+1}''(x) - c_{N+1,1}\phi_{N+1}' - c_{N+1,2}\phi_{N+1}$, so we can substitute for all derivatives of ϕ_N (evaluated at $x = x_0$) in Equation 3.44 to get

$$\begin{aligned} 0 = \sum_{k=0}^{2(N-i)+1} B_{m_i}(N, i, k) & \left(\phi_{N+1}^{(2(N+1-i)+1-k)}(x_0) \right. \\ & - c_{N+1,1}\phi_{N+1}^{(2(N+1-i)-k)}(x_0) \\ & \left. - c_{N+1,2}\phi_{N+1}^{(2(N+1-i)-1-k)}(x_0) \right). \end{aligned}$$

Recall that $B_{m_i}(N, i, 0) = 1$ and $B_{m_i}(N, i, k) = 0$ for $k < 0$ and $k > 2(N - i) + 1$, since it is not possible to sum second indices to get these values. Using these definitions, we may rewrite the sum as

$$\begin{aligned} 0 = \sum_{k=0}^{2(N+1-i)+1} & (B_{m_i}(N, i, k) \\ & - c_{N+1,1}B_{m_i}(N, i, k-1) \\ & - c_{N+1,2}B_{m_i}(N, i, k-2)) \phi_{N+1}^{(2(N+1-i)+1-k)}(x_0). \end{aligned}$$

Finally, we notice that every term in $B_{m_i}(N + 1, i, k)$ either has $c_{N+1,1}$ or $c_{N+1,2}$ or neither in its product. The sum of all terms that do not contain

$c_{N+1,1}$ or $c_{N+1,2}$ is simply $B_{m_i}(N, i, k)$, while the sum of all terms that contain $c_{N+1,1}$ is $-c_{N+1,1}B_{m_i}(N+1, i, k-1)$ and the sum of all terms that contain $c_{N+1,2}$ is $-c_{N+1,2}B_{m_i}(N+1, i, k-2)$. Thus the total sum of all terms in $B_{m_i}(N+1, i, k)$ is

$$B_{m_i}(N+1, i, k) = B_{m_i}(N, i, k) - c_{N+1,1}B_{m_i}(N, i, k-1) - c_{N+1,2}B_{m_i}(N, i, k-2).$$

Substituting this into the previous equation, we get

$$0 = \sum_{k=0}^{2(N+1-i)+1} B_{m_i}(N+1, i, k) \phi_{N+1}^{(2(N+1-i)+1-k)}(x_0)$$

which satisfies the lemma, completing our proof by induction. \square

Since we have two boundary conditions (Equations 3.41 and 3.42) of the form specified in Lemma 3.2 for each ϕ_i in our system, the lemma tells us that we will have two boundary conditions, one at $x = 0$ and one at $x = L$, of order $2k - 1$ for each $k = 1, 2, \dots, N$, giving a total of $2N$ conditions. The set of equations in 3.20 through 3.23 is an example of this result for the two-step model.

These boundary conditions together with the ordinary differential equation provided by Lemma 3.1 give us a general boundary value problem for the N -step model:

$$\begin{cases} 0 = \sum_{k=0}^{2N} C(N, k) \phi_N^{(2N-k)} + \left(\prod_{k=1}^N c_{k,3} \right) \phi_N \\ 0 = \sum_{k=0}^{2N-1} B_{a_1}(N, 2N-1, k) \phi_N^{(2N-1-k)}(0) \\ 0 = \sum_{k=0}^{2N-1} B_{b_1}(N, 2N-1, k) \phi_N^{(2N-1-k)}(L) \\ \vdots \\ 0 = \phi'_N(0) - a_N \phi_N(0) \\ 0 = \phi'_N(L) - b_N \phi_N(L) \end{cases} \quad (3.45)$$

where $c_{i,1} = v_i/D_i$ and $c_{i,2} = \alpha_i/D_i$ for $i = 1, \dots, N$, $c_{i,3} = -\alpha_i R_i/D_i$ for $i = 1, \dots, N-1$, and $c_{N,3} = -\alpha_N R_N/\lambda D_N$.

This boundary value problem allows us to study the principal eigenvalue of the linear operator associated with the combined model, which in turn allows us to determine persistence for the model of N alternating

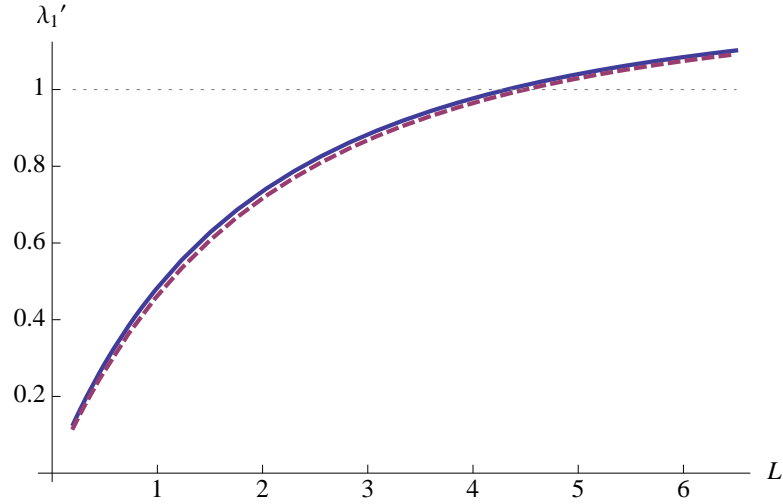


Figure 3.3 The effective principal eigenvalues for the two-step (solid) and three-step (dashed) models as a function of domain length, where $\alpha_1 = \alpha_2 = D_1 = D_2 = 1$, $v_1 = 0.1$, $v_2 = 1$, $R_1 = 1.2$, and $R_2 = 1.5$ for both models and $\alpha_3 = D_3 = 1$, $v_3 = 0.5$, and $R_3 = 1.3$ for the three-step model (solved numerically in Mathematica).

Laplace kernels. Figure 3.3 shows a plot of λ'_1 for the two-step and three-step models as a function of the domain length, demonstrating how numerical solutions to the N -step differential equation and boundary conditions can be used to provide useful information about a given population.

3.3.1 Combinatorics of the Coefficients

The results of Lemmas 3.1 and 3.2 give rise to some interesting combinatorics. For instance, one may quickly notice from a few examples that the number of terms in $C(N, k)$, the coefficient for $\phi_N^{(2N-k)}$, is the same as the number of terms in $C(N, 2N - k)$, the coefficient of $\phi_N^{(k)}$. The coefficients $B_{m_i}(N, i, k)$ also have symmetry in their number of terms. Are there any ways to describe the patterns in the number of terms in the coefficients, and how do these patterns arise?

In fact, the number of terms in $C(N, k)$ is given by $T(N, k)$, the trinomial coefficient that gives the coefficient of x^k in

$$p(x) = (1 + x + x^2)^N$$

(Fahssi, 2012; Sloane, 2013). There are many interpretations of this sequence,

including the number of lattice paths from $(0,0)$ to (N,k) using steps $(1,0)$, $(1,1)$, or $(1,2)$ and the number of ordered trees having $N+1$ leaves at level three and $N+k+3$ edges (Sloane, 2013). An interpretation that allows us to connect $T(N,k)$ to $C(N,k)$ is the number of ways to put k indistinguishable balls in N distinguishable buckets, where no bucket is allowed to have more than two balls (Fahssi, 2012). This relates to our definition of $C(N,k)$ given in Equation 3.33, since here we are summing over N -tuples where each entry is in $\{0,1,2\}$ and the entries sum to k . This corresponds to distributing k indistinguishable "1"s into each of the N entries, where no entry may have more than two "1"s.

The connection to trinomial coefficients inspires another way to write $C(N,k)$:

$$C(N,k) = [x^k](1 - c_{1,1}x - c_{1,2}x^2)(1 - c_{2,1}x - c_{2,2}x^2) \cdots (1 - c_{N,1}x - c_{N,2}x^2)$$

where $[x^k]$ indicates taking the coefficient of x^k in the expanded polynomial. This is the case because when we take cross-terms, no two first indices will be the same, and since the second index matches the power of x , the sum of the second indices in a cross-term will always equal the power of x it multiplies. Since the $c_{i,j}$ are negated, all cross-terms with an even number of $c_{i,j}$ s will be positive and all cross-terms with an odd number will be negative. From this standpoint, it makes sense that the number of terms in $C(N,k)$ is $T(N,k)$, because if we replace every coefficient in the above product with 1, each cross-term contributing to the coefficient x^k will contribute 1 to the sum, thus counting the number of terms.

We can also see the relationship between $C(N,k)$ and $T(N,k)$ in their recurrences. As we derived in the proof of Lemma 3.1, the recurrence for $C(N,k)$ is

$$C(N+1,k) = C(N,k) - c_{N+1,1}C(N,k-1) - c_{N+1,2}C(N,k-2) \quad (3.46)$$

and for $N=1$, we have

$$0 = \phi_1'' - c_{1,1}\phi_1' - c_{1,2}\phi_1 - c_{1,3}\phi_0$$

so we originally have one coefficient in front of each ϕ_n term. The recurrence for the trinomial coefficients is

$$T(N+1,k) = T(N,k) + T(N,k-1) + T(N,k-2)$$

with $T(1,0) = T(1,1) = T(1,2) = 1$ (Sloane, 2013). Since we do not combine any of the coefficients in Equation 3.46, we see that if $T(N,k)$ counts

the number of terms in $C(N, k)$, then $T(N + 1, k)$ will count the number of terms in $C(N + 1, k)$. Since their initial values match up, this is indeed the case.

We can see both from the expression of $C(N, k)$ given in Equation 3.33 and from the definition of $T(N, k)$ that the total number of terms in all of the coefficients will equal

$$\sum_{k=0}^{2N} T(N, k) = 3^N$$

since each element in $\mathcal{S}_N = \bigoplus_{i=1}^N \mathbb{Z}_3$ will contribute one term to a coefficient somewhere in the resulting differential equation (note that the $\mathcal{S}_{N,k}$ partition \mathcal{S}_N).

Similarly, we see that the number of coefficients in $B(N, i, k)$ is also a polynomial coefficient, $T'(N - i, k)$, which gives the coefficient of x^k in

$$q(x) = (1 - x)(1 - x - x^2)^{N-i}.$$

This inspires the representation of $B(N, i, k)$ as

$$B(N, i, k) = [x^k](1 - m_i x)(1 - c_{i+1,1}x - c_{i+1,2}) \cdots (1 - c_{N,1}x - c_{N,2}).$$

From this and Equation 3.43 we see that the total number of terms in all coefficients of either boundary condition of order $2(N - i) + 1 - k$ is

$$\sum_{k=0}^{2(N-i)+1} T'(N - i, k) = 2 \cdot 3^{N-i}.$$

The numbers $T'(N, k)$ have the same recurrence relation as $T(N, k)$, but with initial values $T(0, 2) = 0$ and $T(0, 1) = T(0, 0) = 1$. These initial values correspond to the relationship that for $N = i$, we have

$$0 = \phi'_i(x_0) - m_i \phi_i(x_0)$$

where there is one term in the coefficients for ϕ'_i and ϕ_i , but no coefficient for ϕ''_i .

The relationship to polynomial coefficients is an unexpected but delightful result of Lemmas 3.1 and 3.2.

Chapter 4

Random Kernels

Perhaps one of the most important kinds of time-dependence in nature is randomness. While fixed kernels and growth functions may sometimes be good approximations to model certain populations, in reality almost all aspects of a population's environment and behavior will have some random variability. Thus it is important to explore integrodifference models with random time-dependence.

4.1 Coin-Flip Models

In addition to considering the alternating two-step model, Jacobsen et al. (2013) also consider the "coin-flip" model, in which one of two dispersal kernels, K_1 and K_2 , are chosen with equal probability at each time step.

This model can be extended to an N -sided coin-flip model, in which we have N kernels, K_1, K_2, \dots, K_N and corresponding linearized growth rates R_1, R_2, \dots, R_N , and at each time step t we have

$$n_{t+1}(x) = R_t \int_{\Omega} K_t(x, y) n_t(y) dy$$

where K_t is chosen from one of the N kernels, each with probability $1/N$, and R_t is the growth rate associated to this kernel.

If the N kernels are Laplace kernels, one might ask whether or not this random model has any relationship to the alternating N -step model. For example, since we expect to choose an equal number of each of the kernels in the limit as t goes to infinity, we might expect that the behaviors of these two models will be roughly the same. In fact, Jacobsen et al. (2013) show that for the $N = 2$ case, it appears (based on computer simulations)

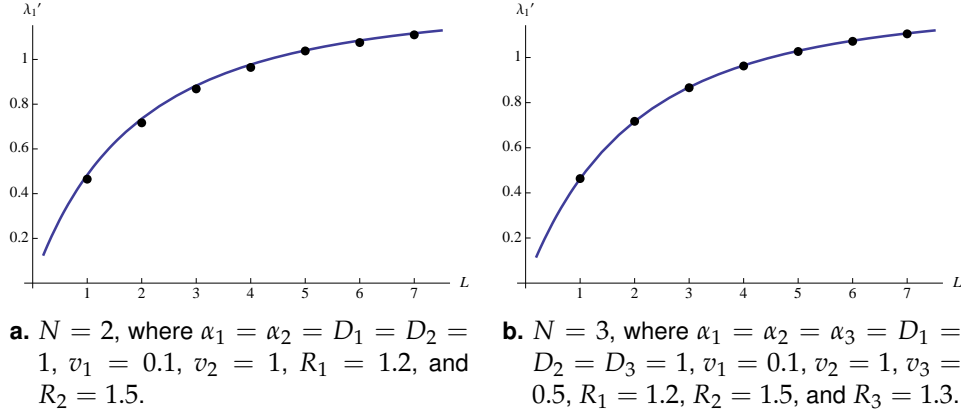


Figure 4.1 The principal eigenvalue λ_1 as a function of domain length for the two- and three-step models, with approximations of Λ for the two- and three-sided coin-flip model plotted at $L = 1, \dots, 7$.

as though the effective eigenvalue Λ of the coin-flip model equals the principal eigenvalue λ_1' if the same two kernels are used.

Using our results for the N -step model and computer simulations to approximate Λ for the N -sided coin-flip model, it appears that this pattern holds for small values of N (see Figure 4.1). Therefore we conjecture that $\Lambda = \lambda_1'$ for the N -sided coin-flip model and the alternating N -step model when the same N Laplace kernels are used for both models. If true, this relationship would allow us to use λ_1' , which can be computed from the results of the previous chapter, to study persistence of populations that follow the random N -sided coin-flip model.

4.2 Laplace Kernels with Random Flow Velocity

Here we derive a recursive solution for $n_t(x)$ for a population under the influence of a randomly varying unidirectional flow, an example first considered by Jacobsen et al. (2013). This solution can be used to write a simulation that models the behavior of the population.

Consider a population living in a domain $\Omega = (-L/2, L/2)$. Suppose that the population disperses according to an asymmetric Laplace kernel with diffusion coefficient D , settling rate α , and time-dependent flow of velocity v_t . Then the dispersal kernel at time t is an asymmetric Laplace

kernel of the form

$$K_t(x, y) = \begin{cases} Ae^{a_t(x-y)} & x < y \\ Ae^{b_t(x-y)} & x \geq y \end{cases} \quad (4.1)$$

where

$$a_t = \frac{v_t}{2D} + \sqrt{\frac{v_t^2}{4D^2} + \frac{\alpha}{D}}, \quad (4.2)$$

$$b_t = \frac{v_t}{2D} - \sqrt{\frac{v_t^2}{4D^2} + \frac{\alpha}{D}}, \quad (4.3)$$

and

$$A = \frac{a_t b_t}{b_t - a_t}$$

as given by Equations 3.2–3.5.

It can be shown by direct integration that for this dispersal kernel, for $\gamma \neq \{a_t, b_t\}$, we have

$$\begin{aligned} \int_{\Omega} K_t(x, y) e^{\gamma y} dy &= \int_x^{L/2} Ae^{a_t(x-y)} e^{\gamma y} dy + \int_{-L/2}^x Ae^{b_t(x-y)} e^{\gamma y} dy \\ &= c_{0,t}(\gamma) e^{\gamma x} + c_{a,t}(\gamma) e^{a_t x} + c_{b,t}(\gamma) e^{b_t x} \end{aligned} \quad (4.4)$$

where the coefficients are defined by

$$\begin{aligned} c_{0,t}(\gamma) &= \frac{a_t b_t}{(\gamma - a_t)(\gamma - b_t)} \\ c_{a,t}(\gamma) &= \frac{a_t b_t}{(b_t - a_t)(\gamma - a_t)} e^{(\gamma - a_t)L/2} \\ c_{b,t}(\gamma) &= \frac{-a_t b_t}{(b_t - a_t)(\gamma - b_t)} e^{(b_t - \gamma)L/2}. \end{aligned}$$

If we assume an initial population density that is constant over the region, say $n_0(x) = 1/L$, then we can use the formula 4.4 above to derive an analytic solution for $n_t(x)$. By the integrodifference model, we have

$$n_{t+1}(x) = R_t \int_{\Omega} K_t(x, y) n_t(y) dy.$$

From 4.4 it is clear that

$$\begin{aligned} n_1(x) &= \frac{R_1}{L} (c_{0,1}(0) + c_{a,1}(0)e^{a_1x} + c_{b,1}(0)e^{b_1x}) \\ &= \frac{R_1}{L} (C_{0,1} + C_{a,1}e^{a_1x} + C_{b,1}e^{b_1x}) \end{aligned} \quad (4.5)$$

where $C_{r,t}$ denotes the coefficient of e^{rx} in $n_t(x)$. We can determine $n_2(x)$ from 4.5 by using Equation 4.4 again on each term of $n_1(x)$, assuming that no two exponentials are the same:

$$\begin{aligned} n_2(x) &= \int_{\Omega} K_2(x, y) n_1(y) dy \\ &= \frac{R_1 R_2}{L} (C_{0,2} + C_{a,2}e^{a_1x} + C_{b,2}e^{b_1x} + C_{a,2}e^{a_2x} + C_{b,2}e^{b_2x}) \end{aligned}$$

where

$$\begin{aligned} C_{0,2} &= C_{0,1}c_{0,2}(0) \\ C_{a,2} &= C_{a,1}c_{0,2}(a_1) \\ C_{b,2} &= C_{b,1}c_{0,2}(b_1) \\ C_{a,2} &= C_{0,1}c_{a,2}(0) + C_{a,1}c_{a,2}(a_1) + C_{b,1}c_{a,2}(b_1) \\ C_{b,2} &= C_{0,1}c_{b,2}(0) + C_{a,1}c_{b,2}(a_1) + C_{b,1}c_{b,2}(b_1). \end{aligned}$$

That is,

$$\begin{bmatrix} c_{0,2}(0) & 0 & 0 \\ 0 & c_{0,2}(a_1) & 0 \\ 0 & 0 & c_{0,2}(b_1) \\ c_{a,2}(0) & c_{a,2}(a_1) & c_{a,2}(b_1) \\ c_{b,2}(0) & c_{b,2}(a_1) & c_{b,2}(b_1) \end{bmatrix} \begin{bmatrix} C_{0,1} \\ C_{a,1} \\ C_{b,1} \end{bmatrix} = \begin{bmatrix} C_{0,2} \\ C_{a,2} \\ C_{b,2} \end{bmatrix}$$

and

$$n_2(x) = \frac{R_1 R_2}{L} (C_{0,2}, C_{a,2}, C_{b,2}, C_{a,2}, C_{b,2}) \cdot (1, e^{a_1x}, e^{b_1x}, e^{a_2x}, e^{b_2x}).$$

In general, $n_t(x)$ can be calculated recursively by

$$n_t(x) = \frac{\prod_{i=1}^t R_i}{L} \mathbf{C}_t \cdot \mathbf{e}_t \quad (4.6)$$

where $\mathbf{e}_t = (1, e^{a_1 x}, e^{b_1 x}, \dots, e^{a_t x}, e^{b_t x})$ and $\mathbf{C}_t = (C_{0,t}, C_{a_1,t}, C_{b_1,t}, \dots, C_{a_t,t}, C_{b_t,t})$, and

$$\begin{bmatrix} c_{0,t}(0) & 0 & & \dots & & 0 \\ 0 & c_{0,t}(a_1) & & & & \\ & & c_{0,t}(b_1) & & & \\ \vdots & & & \ddots & & \vdots \\ & & & & c_{0,t}(a_{t-1}) & 0 \\ 0 & & & & 0 & c_{0,t}(b_{t-1}) \\ c_{a,t}(0) & c_{a,t}(a_1) & c_{a,t}(b_1) & \dots & c_{a,t}(a_{t-1}) & c_{a,t}(b_{t-1}) \\ c_{b,t}(0) & c_{b,t}(a_1) & c_{b,t}(b_1) & \dots & c_{b,t}(a_{t-1}) & c_{b,t}(b_{t-1}) \end{bmatrix} \mathbf{C}_{t-1} = \mathbf{C}_t \quad (4.7)$$

assuming that no two a_t or b_t are the same, which is equivalent to saying that no two flow velocities are the same, since the flow velocity at time t determines a_t and b_t by Equation 4.2 and Equation 4.3. If the flow velocities come from a continuous distribution, this is a reasonable assumption. The recursive formula above allows us to compute not only $n_t(x)$, but also the bound on the effective eigenvalue Λ given in Equation 2.21.

4.2.1 Mathematica Simulation

Using this recursive algorithm, we wrote a Mathematica program to model the population described by this explicit solution (see Appendix D for Mathematica code). The program generates a long list (the length of which can be set by the user) of river flow velocities, each independently selected from a lognormal distribution. This distribution was chosen to ensure that the flow velocity is always positive, thus unidirectional, however another distribution could easily be substituted. The user can set the mean and variance of the flow velocity, as well as the values of the parameters α , D , and L , and the growth rate, R , given by the linearization of the growth function around the zero solution. In this model, we have assumed that the growth function is not time-dependent, so R is the same at each time step. However, the model can be easily adapted so that R is also randomly chosen at each time step.

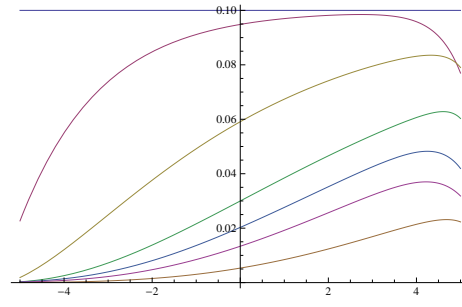
The simulation appears to accurately model the population dynamics for small values of t . In Figure 4.2a, the growth rate R is set to 1, meaning that the population is not growing during the growth stage, but merely remaining the same. Thus we expect the population to go extinct since it is constantly dispersing out of its habitable region and not growing to

compensate for this loss. The figure shows the population density at times $t = 0, 1, \dots, 6$, and it is clear that the population is, in fact, shrinking to zero. Furthermore, we see that the population becomes less dense near the boundaries of its domain, which we expect because there are fewer nearby points within the domain, and because under the Laplace kernel individuals are most likely to disperse to places near their starting locations, so we expect to find fewer individuals near the edges of the domain. Finally, we see in Figure 4.2a that the population becomes skewed to one side of the domain, reflecting the effect of the unidirectional flow.

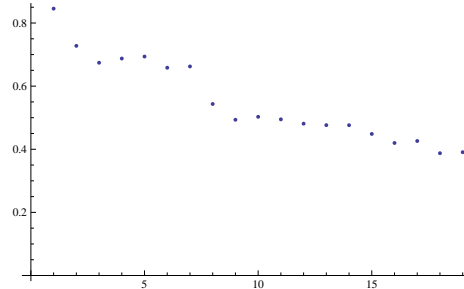
We also see in Figure 4.2b that the approximations for the effective eigenvalue given by $\Lambda_t = [\int_{\Omega} n_t(x) dx]^{1/t}$ appear to be approaching some constant value less than 1 as time increases, as we expect for a population that is dying out. However, for times up to $t = 19$ we do not have enough data to determine an asymptotic value of Λ .

Unfortunately, the model appears to break down for large values of t . In Figure 4.3a we see how the population density begins to show erratic and physically impossible behavior (since it is negative at points, but population densities cannot be negative). This results in poor (and occasionally complex) approximations for Λ in 4.3b, which diverge as t goes to infinity. This unexpected behavior is possibly due to the assumption made in our derivation of Equation 4.6 that no two flow velocities are the same, else we would be dividing by zero. As stated before, since the flow velocities come from a continuous distribution, this is a reasonable assumption. However, in the computer simulation we encounter such an issue. Furthermore, at each recursive step we are dividing by smaller and smaller numbers (differences in flow velocity values), and the program may not be able to accurately complete this kind of computation. The simulation also runs into problems of long run time, which makes it an inconvenient tool for studying this population growth model.

Despite the poor performance of this simulation, it is possible that better numerical methods and computational approaches could lead to a more accurate simulation. Such a simulation would allow us to gather useful information about a given population and help us make conjectures about properties such as the dependence of Λ on the flow velocity mean and variance.

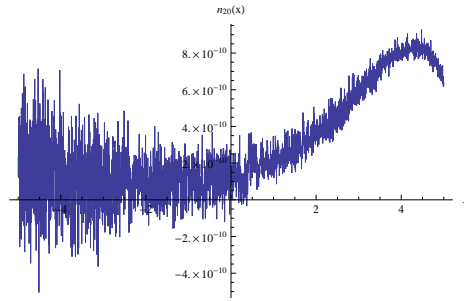


a. A plot of the population densities on $(-5, 5)$ for $t = 0, \dots, 6$. The flat line at the top is $n_0(x)$ and the population shrinks at each successive time step, as we expect since Λ appears to converge to a value less than 1.

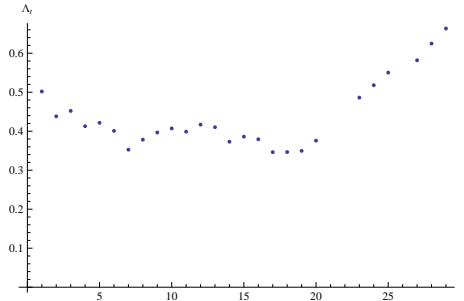


b. A plot of successive approximations of Λ using equation (2.19) for $t = 0, \dots, 19$. It appears as though the sequence of approximations is converging to some value less than 1 as $t \rightarrow \infty$, indicating the population will go extinct.

Figure 4.2 The plots above were generated using my simulation. Both plots are from the same set of randomly generated flow velocities with mean and variance 1. In both plots, the parameter values used were $\alpha = D = R = 1$ and $L = 10$.



- a.** A plot of the population density at $t = 20$. The graph displays wild behavior and is negative at points in the domain, indicating that the simulation is failing to accurately calculate the population density.



- b.** A plot of successive approximations of Λ for $t = 0, \dots, 30$. After around $t = 20$, the values stop appearing to converge and instead go off to infinity. Missing points indicate that the value calculated by the simulation were complex.

Figure 4.3 As in Figure 4.2, both plots above were calculated with a flow velocity mean and variance of 1, $\alpha = D = R = 1$, and $L = 10$. The plots above were generated from a different set of flow velocities than those in Figure 4.2.

Chapter 5

Discussion

In this paper we have explored a number of time-dependent integrodifference population models and developed tools for gleaning useful information from these models. First, we established the inequality $\Lambda \leq r$ in Theorem 2.1, which implies that $\Lambda > 1$ is a sufficient condition for persistence of a population. Then we derived a $2N^{\text{th}}$ -order boundary value problem with $2N$ boundary conditions that allow us to determine the principal eigenvalue for a model with N alternating asymmetric Laplace dispersal kernels. We explored the relationship between the alternating N -step model and the N -sided coin-flip model, in which one of N Laplace kernels is chosen randomly at each time step, and conjectured that Λ for the coin-flip model will equal the effective principal eigenvalue λ'_1 for the alternating model if the same N kernels are used. Finally, we used an explicit recursive solution to create a simulation for a population that disperses according to Laplace kernels with randomly chosen flow velocities at each time step. Although the simulation breaks down for large time values, this approach can potentially be adapted to yield useful information about random time-dependent integrodifference models.

There are many future directions of study suggested by this research. It remains to be verified whether or not $\Lambda = \lambda'_1$ for corresponding N -step and N -sided coin-flip models. A better simulation could be used to probe the relationship between the mean and variance for a variety of parameters and the resulting effective eigenvalue for completely random kernels. Does the relationship depend on the initial population? Does it depend on the distribution parameters are chosen from? In addition, the analysis of the N -step alternating Laplace kernels could be carried out for a variety of other common dispersal kernels, such as a Gaussian.

Integrodifference population models are of great importance in analyzing the dynamics of species that have separate growth and dispersal stages. Developing the theory of time-dependence is essential to create more realistic models, providing ecologists with greater flexibility to choose models that are more accurate for the specific populations they study. This research develops a number of tools for studying time-dependent models, with the ultimate goal of aiding the conservation of valuable species and ecosystems.

Appendix A

Fréchet Derivative of the Nonlinear Hammerstein Operator at Zero

Theorem A.1. *Let F be the nonlinear Hammerstein operator defined by*

$$F[u] = \int_{\Omega} K(x, y) f(u(y)) dy$$

for all $u \in C(\overline{\Omega})$, where Ω is a bounded subset of \mathbb{R}^n , K is continuous on $\overline{\Omega} \times \overline{\Omega}$, and f is differentiable at zero. Then the Fréchet derivative of F at zero is \mathcal{L} defined by

$$\mathcal{L}u = f'(0) \int_{\Omega} K(x, y) u dy.$$

Proof. To find the Fréchet derivative of F at zero, we examine

$$F[h] - F[0] = \int_{\Omega} K(x, y) f(h) dy - \int_{\Omega} K(x, y) f(0) dy. \quad (\text{A.1})$$

Since f is differentiable at zero, we know $f(h) = f(0) + f'(0)h + r(h)$ where $r(h)$ is a remainder such that $\|r(h)\|_{\infty} / \|h\|_{\infty} \rightarrow 0$ as $\|h\|_{\infty} \rightarrow 0$ (Ambrosetti and Prodi, 1993). Thus Equation A.1 becomes

$$\begin{aligned} F[h] - F[0] &= \int_{\Omega} K(x, y) (f(0) + f'(0)h + r(h)) dy - \int_{\Omega} K(x, y) f(0) dy \\ &= f'(0) \int_{\Omega} K(x, y) h dy - \int_{\Omega} K(x, y) r(h) dy \\ &= \mathcal{L}h - R[h] \end{aligned}$$

where $\mathcal{L}h = f'(0) \int_{\Omega} K(x, y) h \, dy$ is linear in h and the remainder $R[h]$ satisfies

$$\begin{aligned} \frac{\|R[h]\|_{\infty}}{\|h\|_{\infty}} &= \frac{\left\| \int_{\Omega} K(x, y) r(h) \, dy \right\|_{\infty}}{\|h\|_{\infty}} \\ &\leq \frac{\int_{\Omega} \|K(x, y)\|_{\infty} \|r(h)\|_{\infty} \, dy}{\|h\|_{\infty}} \\ &= \frac{\|r(h)\|_{\infty}}{\|h\|_{\infty}} |\Omega| \|K(x, y)\|_{\infty} \rightarrow 0 \end{aligned}$$

as $\|h\|_{\infty} \rightarrow 0$ since $\|r(h)\|_{\infty} / \|h\|_{\infty} \rightarrow 0$ and $|\Omega| \|K(x, y)\|_{\infty}$ is bounded. We know this quantity is bounded because Ω is bounded and because K is a real, continuous function defined on a closed and bounded (thus compact) set in \mathbb{R}^n , so it is also bounded.

Since $F[h] = F[0] + \mathcal{L}h + R[h]$ where $\|R[h]\|_{\infty} / \|h\|_{\infty} \rightarrow 0$ as $\|h\|_{\infty} \rightarrow 0$, we have that \mathcal{L} is the Fréchet derivative of F at zero (Ambrosetti and Prodi, 1993). \square

Appendix B

Contraction Mapping Principle for the Operator T

Theorem B.1. Define the linear operator $T : C(\overline{\Omega}) \rightarrow C(\overline{\Omega})$ by

$$Tu(x) = \frac{R}{\lambda} \int_{\Omega} K(x, y)u(y)dy$$

where $R \in \mathbb{R}$, Ω is a bounded subset of \mathbb{R}^n , and K is continuous on $\overline{\Omega} \times \overline{\Omega}$. For $\lambda > R|\Omega| \|K\|_{\infty}$, T is a contraction mapping and has unique fixed point, $u = 0$.

Proof. To see that T is a contraction under this condition, notice that

$$\begin{aligned} \|Tu_2 - Tu_1\|_{\infty} &= \left\| \frac{R}{\lambda} \int_{\Omega} K(x, y)u_2(y)dy - \frac{R}{\lambda} \int_{\Omega} K(x, y)u_1(y)dy \right\|_{\infty} \\ &= \left\| \frac{R}{\lambda} \int_{\Omega} K(x, y)(u_2(y) - u_1(y))dy \right\|_{\infty} \\ &\leq \frac{R}{\lambda} \int_{\Omega} \|K\|_{\infty} \|u_2 - u_1\|_{\infty} dy \\ &= \frac{R|\Omega| \|K\|_{\infty}}{\lambda} \|u_2 - u_1\|_{\infty}. \end{aligned}$$

Recall from Appendix A that $\|K\|_{\infty}$ is bounded. Thus for $\lambda > R|\Omega| \|K\|_{\infty}$ we have

$$\|Tu_2 - Tu_1\|_{\infty} \leq M \|u_2 - u_1\|_{\infty}$$

where $M < 1$, making T a contraction mapping.

By the contraction mapping theorem, any contraction has a unique fixed point. We may see by inspection that $u = 0$ is a fixed point of T , thus for large enough λ , this is the unique fixed point of T . \square

Appendix C

Positivity, Boundedness, and Compactness of the Linearization

Theorem C.1. *Let the linear operator $\mathcal{L} : C(\overline{\Omega}) \rightarrow C(\overline{\Omega})$ be defined by*

$$\mathcal{L}u(x) = R \int_{\Omega} K(x, y)u(y)dy$$

where $R \in \mathbb{R}$, $R \geq 0$, Ω is a bounded subset of \mathbb{R}^n , and K is continuous on $\overline{\Omega} \times \overline{\Omega}$. Then \mathcal{L} is a positive, bounded, compact operator.

Proof. Since $K \geq 0$ and $R \geq 0$, and the integral of a nonnegative function is nonnegative, \mathcal{L} takes nonnegative functions to nonnegative functions, and is therefore a positive operator.

We can also see that \mathcal{L} is bounded, since

$$\begin{aligned} \|\mathcal{L}u\|_{\infty} &= \left\| R \int_{\Omega} K(x, y)u(y)dy \right\|_{\infty} \\ &\leq R \int_{\Omega} \|K\|_{\infty} \|u\|_{\infty} dy \\ &= R|\Omega| \|K\|_{\infty} \|u\|_{\infty} \end{aligned}$$

where we recall from Appendix A that K is bounded and that we are working in a bounded domain. Thus \mathcal{L} is a bounded operator.

Finally, we show that \mathcal{L} is compact. A compact operator on a Banach space takes bounded subsets to precompact sets (sets where the closure is compact), or equivalently, the image of any bounded sequence under a compact operator has a convergent subsequence.

Consider any bounded sequence of functions $\{u_k\} \in C(\overline{\Omega})$, where say $\|u_k\|_\infty < M$ for all k . Since \mathcal{L} is a bounded operator, the image of this sequence, $\{\mathcal{L}u_k\}$, is pointwise bounded. For any $\mathcal{L}u_k$ in this sequence and any $x_1, x_2 \in \Omega$, consider

$$\begin{aligned} |\mathcal{L}u_k(x_2) - \mathcal{L}u_k(x_1)| &= \left| R \int_{\Omega} K(x_2, y) u_k(y) dy - R \int_{\Omega} K(x_1, y) u_k(y) dy \right| \\ &= \left| R \int_{\Omega} (K(x_2, y) - K(x_1, y)) u_k(y) dy \right| \\ &\leq R \int_{\Omega} |K(x_2, y) - K(x_1, y)| |u_k| dy \\ &< RM \int_{\Omega} |K(x_2, y) - K(x_1, y)| dy. \end{aligned}$$

Since K is continuous on a compact set, it is uniformly continuous, which implies that for any $\epsilon > 0$, there exists a $\delta > 0$ such that

$$|(x_2, y) - (x_1, y)| = |x_2 - x_1| < \delta$$

implies that

$$|K(x_2, y) - K(x_1, y)| < \frac{\epsilon}{RM|\Omega|}$$

for any y . Thus $|x_2 - x_1| < \delta$ implies that

$$\begin{aligned} |\mathcal{L}u_k(x_2) - \mathcal{L}u_k(x_1)| &< RM \int_{\Omega} \frac{\epsilon}{RM|\Omega|} dy \\ &= \epsilon \end{aligned}$$

for any u_k and any $x_1, x_2 \in \Omega$. Thus $\{\mathcal{L}u_k\}$ is equicontinuous.

By the Arzelà-Ascoli theorem, since $\{\mathcal{L}u_k\}$ is pointwise bounded and equicontinuous, it has a uniformly convergent subsequence. Thus \mathcal{L} is a compact operator.

□

Appendix D

Mathematica Code Simulating a Random Model

Here we present Mathematica code implementing an explicit recursive solution derived in Section 4.2 for a population that disperses according to an asymmetric Laplace kernel with randomly varying flow velocity. Each time the program is run, it randomly generates flow velocities from a log-normal distribution and uses them to compute $n_t(x)$ and an approximation for Λ (these are the last two functions). The user can set parameter values at the top of the code.

```
Clear[a, b, c, c0, ca, cb, e, L, mean1, mean2, var1, var2, n, x, t, c0List, caList, cbList,
      cMatrix, R, K, Lambda, alpha, Disp, vel, cList, eList, maxIndex, velocity];

L = 10;
mean1 = .5;
var1 = 1;
mean2 = .5;
var2 = .5;
R = 7;
alpha = 1;
Disp = 2;
maxIndex = 200;

velocity[0] = {};
velocity[i_] := Append[velocity[i - 1], RandomVariate[LogNormalDistribution[mean1, var1]]];
vel = velocity[maxIndex];

a = Table[Part[vel, i] / (2 Disp) + (vel[[i]]^2 / (4 Disp^2) + alpha / Disp)^0.5, {i, maxIndex}];
b = Table[Part[vel, i] / (2 Disp) - (Part[vel, i]^2 / (4 Disp^2) + alpha / Disp)^0.5, {i, maxIndex}];

c0[i_, gam_] = a[[i]] b[[i]] / ((gam - a[[i]]) (gam - b[[i]]));
ca[i_, gam_] = Exp[L (gam - Part[a, i]) / 2] Part[a, i]
               Part[b, i] / (Part[b, i] - Part[a, i]) / (gam - Part[a, i]);
cb[i_, gam_] = -Exp[L (Part[b, i] - gam) / 2] Part[a, i]
               Part[b, i] / (Part[b, i] - Part[a, i]) / (gam - Part[b, i]);
c0List[j_] =
  Join[{c0[j, 0]}, Riffle[Table[c0[j, Part[a, i]], {i, j - 1}], Table[c0[j, Part[b, i]], {i, j - 1}]]];
caList[j_] =
  Join[{ca[j, 0]}, Riffle[Table[ca[j, Part[a, i]], {i, j - 1}], Table[ca[j, Part[b, i]], {i, j - 1}]]];
cbList[j_] =
  Join[{cb[j, 0]}, Riffle[Table[cb[j, Part[a, i]], {i, j - 1}], Table[cb[j, Part[b, i]], {i, j - 1}]]];
cMatrix[j_] = Insert[Insert[DiagonalMatrix[c0List[j]], caList[j], 2 j], cbList[j], 2 j + 1];

c[0] = {1};
c[t_] = cMatrix[t].c[t - 1];

e[x_, 0] = {1};
e[x_, t_] = Insert[Insert[e[x, t - 1], Exp[Part[a, t] x], 2 t], Exp[Part[b, t] x], 2 t + 1];

n[t_, x_] := c[t].e[x, t] / L;

Lambda[t_] := (Integrate[n[t, x], {x, -L/2, L/2}])^(1/t);
```

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